

SEX ANOMALIES IN THE GENUS ASHMEADIELLA
(HYMENOPTERA) WITH NOTES ON THE HOMOLOGIES
BETWEEN MALE AND FEMALE GENITAL APPENDAGES

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Comparable sex anomalies of two different species of the genus *Ashmeadiella* [*A. (Ashmeadiella) opuntiae* (Cockerell) and *A. (Chilosima) rhodognatha* Cockerell] were collected in the desert portion of Riverside County, California, during the spring of 1936. Both individuals are bilaterally symmetrical and present a blending of male and female characteristics, with, in addition, certain features common to both intersexes but not found in normal specimens of either sex. The two anomalous individuals are primarily female although the mandibles are of a modified male type and the claws are cleft as in males. The sixth abdominal terga show at least suggestions of the dentation found in normal males (figs. 5 and 10). The clypeus of each is abnormally produced, with its anterior margin thickened and crenulate (figs. 2 and 8), in a manner different from normal individuals of either sex. Furthermore, the mandibles are shorter than in either sex and have a large rounded, somewhat irregular thickening or tubercle, not found in either sex, on their outer surfaces immediately basad of the teeth. It is an interesting suggestion that these two similarly anomalous specimens collected in the same area at virtually the same time may have been the result of comparable environmental conditions of some sort.

More complete descriptions of the characteristics which vary intersexually are given below. Unfortunately, from the standpoint of an examination of internal organs, both specimens were pinned and dried before their anomalous features were observed.

ASHMEADIELLA RHODOGNATHA COCKERELL

Facial pubescence as dense as in female; antennae twelve-segmented as in female; clypeus more strongly produced than in either sex, its apical margin thickened, irregularly undulate; mandibles tridentate, strongly thickened just before teeth, shorter than those of normal male; mesocutum rather coarsely punctate as in female; tarsal claws cleft, as in male; sixth tergum (morphological seventh) with posterior margin strongly bilobed medi-

ally and with a small lobe at either side (thus intermediate between male and female); abdominal sterna without scopa, the fourth (morphological fifth) with three small lobes along its posterior margin, which is entire in normal specimens of both sexes; sterna beyond the sixth absent, as in female. The peculiar seventh and eighth terga and genitalia are discussed below.

Five miles west of Indio, Riverside County, California, April 10, 1936, on flowers of *Prosopis chilensis*, collected by the author.

ASHMEADIELLA OPUNTIAE (COCKERELL)

Similar to normal female, antennae being twelve-segmented; clypeus more strongly produced and more broadly truncate than in either sex, its apical margin thickened and irregularly undulate; mandibles slightly shorter than in normal male, thickened and tuberculate just before teeth, apices bidentate, inner tooth small; tarsal claws cleft, as in male; sixth (morphological seventh) tergum similar to that of female but with four feeble lobes, suggesting the characteristic teeth of the male; sternal scopa present, somewhat sparse; sting and associated organs as in female.

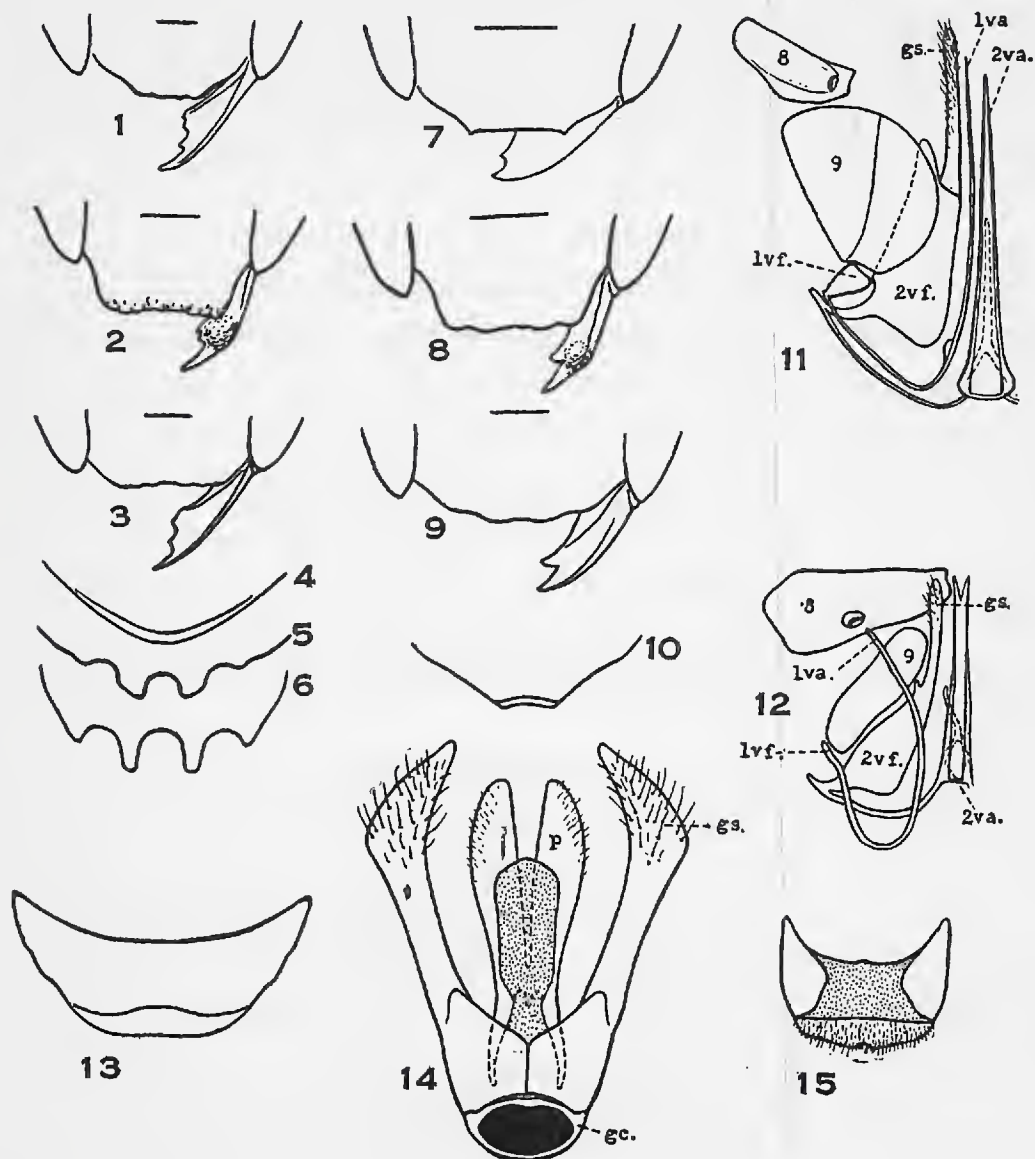
Cathedral City, Riverside County, California, April 9, 1936, on *Echinocactus cylindraceus*, collected by Dr. E. G. Linsley to whom I am indebted for the opportunity to study this specimen.

As may be seen from these descriptions, the specimen of *opuntiae* closely approaches the normal female, while that of *rhodognatha* falls near the midpoint between the two sexes. It may be supposed that each intersex developed as one sex for a part of its life, after which it developed as the opposite sex.

A study of the genital structures of the intersexual individual of *rhodognatha*, in which these parts are involved in the anomaly, is highly interesting and possibly significant in establishing the homologies of these parts. Since many other structures of the insect present a condition intermediate between that of the male and that of the female, it may be assumed that the genital structures, being different from those of the normal female, also approach the condition found in the male.

A superficial examination indicates that this supposition is correct. As will be seen from a study of figures 11 and 12, the eighth (counting the propodeum as first) tergum is larger and its parts more closely approximate in the intersex than in a normal female, while the ninth tergum is smaller than in the normal

female. Both of these are modifications in the direction of maleness. In the intersex the first valvifers are much reduced in size,



EXPLANATION OF FIGURES

1. Lower portion of face of *Ashmeadiella rhodognatha* Cockerell, female. 2, Same, intersex. 3, Same, male.
4. Apex of seventh tergum of *Ashmeadiella rhodognatha* Cockerell, female. 5, Same, intersex. 6, Same, male.
7. Lower portion of face of *Ashmeadiella opuntiae* (Cockerell), female. 8, Same, intersex. 9, Same, male.
10. Apex of seventh tergum of *Ashmeadiella opuntiae* (Cockerell), intersex.
11. Sting and associated structures (omitted on right side) of *Ashmeadiella*, female.

and instead of actually articulating with the ninth tergum and second valvifers, their angles merely approach the points of articulation on these sclerites and are separated from them by small membranous intervals. Furthermore, the first valvulae are blunt and loosely curled anteriorly, not forming stylets in the sting. If these reductions are in the direction of the male, it may be assumed that the first valvifers and valvulae disappear in the male, and it is true that no homologues of these structures are present in that sex, the eighth abdominal segment, as in other male Pterygota, being devoid of appendages. The second valvifers of the intersex lack the usual posterior processes and articulate with the second valvulae directly at their posterior inner angles. The third valvulae are immovably fused at the extreme anterior ends of the second valvifers, although in the female they are articulated subapically. The second valvulae are fused and swollen basally, somewhat as in the female, but are slightly separated at the apices.

The appendages of the ninth abdominal segment, that is, the second valvifers with the second and third valvulae, in this intersexual individual bear a strong resemblance to the genital armature of the male (figure 14). If this resemblance indicates homology (and from the standpoint of position with regard to adjacent sclerites there is no reason to believe that it does not), the basal ring (cardo) must represent the fused basal parts of the coxopodites (second valvifers) of the ninth abdominal segment. The claspers or lateral portions of the male genital armature, two-segmented in most Hymenoptera but fused into un-

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12. Eighth and ninth terga and appendages of eighth and ninth segments (omitted on right side) of *Ashmeadiella rhodognatha* Cockerell, intersex.
 13. Eighth tergum of *Ashmeadiella*, male.
 14. Genitalia of *Ashmeadiella*, male, ventral view, apex upward to correspond to positions of genital appendages of female and intersex.
 15. Ninth tergum of *Ashmeadiella*, male.

8, eighth hemitergite; 9, ninth hemitergite; *1vf.*, first valvifer; *1va.*, first valvula; *2vf.*, second valvifer; *2va.*, second valvulae; *gs.*, gonostylus; *gc.*, gonocardo; *p.*, penis valve. Abdominal segments are numbered with the propodeum as one, the first metasomal segment as two.

jointed organs in the Megachilidae, represent the remainders of the second valvifers and the third valvulae; the third valvulae of the female are thus the homologues of the styli (or parameres of Snodgrass, 1941, *Smithsonian Misc. Coll.*, 99(14):18) of the male genitalia. Furthermore the penis valves or sclerotizations of the median part of the male genitalia may be homologous to the second valvulae of the female. Thus, in contrast to recent opinions (Snodgrass, 1935, *Principles of insect morphology*, ix + 667 pp., 319 figs., McGraw-Hill Book Co.; 1941, *Smithsonian Misc. Coll.*, 99(14):1-86, 6 figs., 33 pls.) all these sclerotic organs would be regarded as periphallic and appendicular in origin, and the membranous intromittent organ itself is the only phallic structure in the male genitalia of the Hymenoptera.

Popov (1935, *Rev. Ent. U.R.S.S.*, p. 162) figures the genitalia of a specimen of *Andrena* in which all the female structures were present and in addition the male genital structures of the right side of the body. This suggests that the entire male genital apparatus is phallic in origin since the appendage of the right side of the ninth abdominal segment could hardly produce both male and female structures complete. However, too much weight should not be placed on such an asymmetrical monstrosity, and indeed Popov (1937, *Bull. Acad. Sci. U.R.S.S.*, pp. 487-498) in another paper gives figures of a gynandromorphic *Halictus* which suggests the same homologies between male and female genital structures as are indicated by the intersexual *Ashmediella*.

These same homologies have also been strongly supported by comparative studies of the structures of other insects which will be reported upon in another paper. They are summarized thus:

FEMALE	MALE
first valvifer	absent
first valvula (gonapophysis)	absent
second valvifer	cardo and gonocoxite (or basal segment of outer clasper)
second valvula (gonapophysis)	penis valve?
third valvula or gonostylus	gonostylus (or distal segment of outer clasper)